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# CLAYTONIA GRONOV.

## A MORPHOLOGICAL AND ANATOMICAL STUDY.

BY

**THEODORE HOLM.**

PRESENTED TO THE ACADEMY BY GEORGE L. GOODALE.

# CLAYTONIA GRONOV. A MORPHOLOGICAL AND ANATOMICAL STUDY.

By **Theo. Holm.**

(With plates 1 and 2.)

## I. CLAYTONIA AS A GENUS.

A glance at the literature and a consideration of the species themselves must necessarily convince even the most critical systematist that *Claytonia*, as heretofore defined, can not possibly be confounded with *Montia*, nor *Montia* with *Claytonia*. They both have been excellently described and seemingly well understood now for at least a century and a half.

Sometimes the accumulation of new material with additional new species may alter the views of the systematist in regard to the proper limitation of some genus, but this has not been the case with *Claytonia*. From the skillful treatment of such eminent systematists as **Fenzl** and **Gray**, the genus has been received and explained as it always was, and has, of course, been kept separate from the monotypic *Montia*. Though by no means a large genus, indeed rather a small one, *Claytonia* represents an assemblage of species of marked variation in habit but with the floral structure principally the same. As classified by **Gray**,[a] the species are divided into five sections based upon characters derived from the vegetative organs mainly: *Euclaytonia*, the large-rooted *C. megarrhiza*, *C. Virginica*, etc.; *Limnia*, the fibrous-rooted annual or perennial *C. Sibirica*, *C. perfoliata*, etc.; *Alsinastrum*, the stoloniferous *C. Chamissonis; Naiocrene*, the bulbiferous *C. parvifolia*, and finally *Montiastrum*, the leafy-stemmed and alternate-leaved annuals *C. diffusa* and *C. linearis*, of which the latter is, furthermore, distinct by the flowers having the petals obviously unequal, but unguiculate as in the other species, and by the number of stamens being sometimes reduced to only three.

While thus the vegetative organs exhibit a very pronounced variation in *Claytonia*, the floral structure appears essentially the same. The position of the calyx leaves is the same in all the species enumerated by **Gray**, the anterior covering the posterior. The petals are always prominently unguiculate and more or less coherent at the very base; their relative length may be somewhat different within the same flower, as noticed in *C. linearis*. The stamens, normally five, are inserted near the base of the petals, and finally the ovary is ovoid, bearing a long style with three short branches, papillose only on their inner surface. It will be seen from this that the flower of *Claytonia* throughout the genus—from *Euclaytonia* to *Montiastrum*, inclusive—shows the same diagram, and that the modification sometimes observable in the relative size of the petals and in the number of stamens does not disturb the primary arrangement of the individual parts of the flower.

It is now surprising to see that, notwithstanding such uniformity in floral structure, *Claytonia* has in late years[b] been divided and a number of its species been referred to *Montia*, with which they have nothing in common. Here again the literature and a renewed examination of *Montia* would have shown what *Montia* is and how correctly it was described and understood by Linnæus. Let us then recapitulate some of the most essential points in the flower by which the monotypic *Montia* differs from "all the other genera of the order *Portulacaceæ*." The exactly opposite arrangement of the calyx leaves, the posterior of these covering the anterior;[a] the somewhat zygomorphic, gamopetalous corolla with the three stamens inserted at the apex of the corolla tube; the turbinate ovary with a minute style and three long, subplumose stigmata. Having advanced these brief remarks upon the generic characters of *Claytonia* and *Montia*, we might now proceed to describe some morphological and anatomical points in *Claytonia*, and, of course, we receive the genus in the same way as it was understood before and outlined so well in the works of GRAY, FENZL, JUSSIEU, BENTHAM and HOOKER, ENGLER and PRANTL, etc.

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[a] Proceed. Am. Acad., New Ser., Vol. 14, 1887, p. 278.

[b] Synoptical Flora of North America, Vol. I, 1895–97, p. 272.

## II. THE INFLORESCENCE.

The aerial stems are in *Claytonia* nearly always terminated by an inflorescence, usually preceded by one pair of opposite leaves, which by WYDLER and EICHLER have been defined as foreleaves; the flowers themselves are mostly destitute of such foreleaves, but there are species in which one of these, the fertile, is readily visible as a minute bract, especially in the lower portion of the inflorescence. Frequently the foreleaves are the only leaves of the aerial stems, but in some few species the stems are quite leafy from the base to the inflorescence in *C. Chamissonis* ESCH., where the leaves are opposite, while in *C. linearis* DOUGL. and *C. parvifolia* MOC. they are alternate.

In regard to the inflorescence, this is of the cymose type, but seems never to be regularly or completely developed in our genus. It sometimes begins as a very regular cyme, but the lateral ramifications soon turn to monochasia of the type cicinnus or scorpioid cyme, as described by WYDLER[b]. Most complete is the cyme perhaps in *C. Sibirica* L.; the stem is terminated by a flower, and a lateral inflorescence is developed in the axil of each of the two prophylla. The one of these lateral inflorescences may continue this regular cymose ramification at least at intervals, while the other, usually very soon, turns to a monochasium; nearly all the flowers are in this species provided with one of the two foreleaves (the fertile), but they are relatively small, especially in the monochasia. A like composition of the inflorescence may also be observed in *C. sarmentosa* MEY., but in most of the specimens examined of this species a few-flowered scorpioid cyme seemed to be the typical. In large specimens of *C. linearis* DOUGL., the inflorescence begins as a cyme, but the lateral branches become immediately leafless monochasia of the same type as described above; in small specimens, on the other hand, only one prophyllon is developed, and the inflorescence consists only of one or four flowers representing a true monochasium.

Partly a true cyme and partly a scorpioid cyme is the inflorescence of *C. megarrhiza* PARRY and *C. arctica* ADAMS; an apparently regular cyme is to be found in *C. Chamissonis*, ESCH., at least in the lower portion, but while the one lateral branch becomes a four or five flowered leafless monochasium, the other most frequently develops as a long vegetative shoot. In the other species which we have examined a scorpioid cyme is the only kind of inflorescence represented, mostly with the secondary prophylla entirely suppressed, as in *C. Virginica* L., *C. Caroliniana* MICHX., *C. asarifolia* BONG., *C. parviflora* DOUGL., *C. lanceolata* PURSH, *C. gypsophiloides* FISCH. et MEY., *C. spathulata* DOUGL., and *C. arenicola* HEND.; the last species possesses long, many-flowered monochasia in which all the flowers are provided with a prophyllon. In *C. parvifolia* MOC. the inflorescence has only very few flowers, since the one of the two lateral branches, as it seems, constantly develops into a vegetative shoot; this species is, furthermore, peculiar by the two opposite prophylla being developed only as minute, hyaline, and scale-like leaves, besides that the numerous stem leaves subtend small bulblets, which are said to fall off and to develop new individuals.

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[a] Almquist S. Om blomdiagrammet hos *Montia* (Botan. Notiser 1884: 156, and Botan. Centralbl. 21:91. 1885). The fruit and the seeds in *Montia*, as well as the mechanism by which the seeds are ejected, is carefully described by Professor Urban (Jahrb. bot. Garten Berlin 4:256, 1886).

[b] Flora, 1851: 348.

## III. THE MORPHOLOGICAL STRUCTURE OF THE SHOOT.

The primary shoot represents a monopodium in nearly all the species. The main axis bears in these only leaves, which are always green and developed as proper leaves; it is from the axils of these that the flower-bearing stems develop in the first year, when the species is an annual, but much later if it is a perennial. A rhizome is often developed and in a very different manner, which depends not only upon the structure of the rhizome itself, but also upon the structure of the root system. The species of *Claytonia* exhibit altogether a striking diversity as far as concerns their mode of growth, and it is strange to see how differently certain species behave in this respect, although they are otherwise to be considered as near allies. A classification of the species from a biological view point must, therefore, result in the separation of related types, at least in some instances.

These biological types may be arranged as follows:

### 1. ANNUALS.

A.—The shoot is terminated by an inflorescence (*C. linearis* Dougl., *C. diffusa* Nutt., *C. dichotoma* Nutt.).

B.—The apex of the shoot is vegetative, represented by a rosette of leaves (*C. Sibirica* L., *C. arenicola* Hend., *C. perfoliata* Dow., *C. parviflora* Dougl., *C. gypsophiloides* Fisch. et Mey., *C. spathulata* Dougl.).

### 2. PERENNIALS.

C.—As B, but with a fleshy, horizontal rhizome and filiform secondary roots (*C. asarifolia* Bong.).

D.—As C, but the rhizome is very short and slender, and bulblets are developed in the axils of the stem leaves. (*C. parvifolia* Moc.).

E.—Monopodial, as those above (from B to D inclusive), but the rhizome is erect and short with a very large root, the primary (*C. Virginica* L., *C. Caroliniana* Michx., *C. lanceolata* Pursh, *C. megarrhiza* Parry, *C. arctica* Adams).

F.—Monopodial, with stolons above ground and slender root (*C. sarmentosa* Mey.).

G.—Not monopodial, with filiform roots and stolons underground, often terminated by bulblets. (*C. Chamissonis* Esch.).

Seven well-marked biological types are thus characteristic of these eighteen species of *Claytonia*. Let us examine these a little further.

Among the annuals, *C. linearis* Dougl., *C. diffusa* Nutt., and *C. dichotoma* Nutt., it appears as if the primary axis becomes continued into an inflorescence. We use the expression "appears" since the material which we have examined was not quite sufficient or satisfactory for this purpose; moreover, only dried specimens were at our disposal. The larger specimens were profusely branched in the first of these species, and the true ramification could not be made out beyond that the leaves were all alternate and that there was no trace of any basal rosette, so very distinct and readily observable in all the other annuals of the section B. In some small specimens the cotyledons were still preserved, and they were linear and above ground. Only two inflorescences were developed in these specimens, and from the same height, and either were both axillary and pertaining to the cotyledons, or the one was axillary and the other one terminal. The latter explanation seems to be the more probable, inasmuch as there was no evidence of any rudimentary terminal bud. However, a renewed examination of fresh material may prove the opposite.

All the other annuals which we have examined possessed a rosette of leaves from the axils of which the flower-bearing stems had developed. The primary root is long and slender. *Claytonia Sibirica* L. belongs to this category, but it appears as if this species also occurs as perennial, judging from a note in Gray's paper cited above. This author states that it is "a pure annual when it grows in exsiccated soil, but when better nourished it is more enduring and bears offsets on stout stolons from the crown, and so, in the absence of much winter's cold, its life is continued and extended from year to year." We have not been able to secure any material that showed such modification, but it is interesting to know that a perennial form does exist of this species, and that it is stoloniferous; in certain other genera and of remote orders similar perennial and stoloniferous specimens have been recorded of species that are otherwise typically annual.[a]

The next large group (2) comprises such species as are typically perennial, and the first of these, *C. asarifolia* BONG., possesses a horizontally creeping and quite fleshy rhizome, the apex of which bears a number of large leaves with axillary inflorescences. The primary root has vanished and is replaced by many filiform secondary ones, which proceed from the very short internodes of the rhizome. A like but much more slender rhizome is developed in *C. parvifolia* MOC., a species that is very characteristic by its alternate stem leaves and by the presence of bulblets in the axils of these. The bulblets resemble very much those of *Dentaria bulbifera*, *Saxifraga cernua*, etc. (Pl. 1, fig. 1.) We now pass to section E, in which the rhizome is vertical and very short, but in which the primary root sometimes attains an enormous development. To here belong *C. megarrhiza* PARRY, *C. Virginica* L, and their allies. Of these the former is the most remarkable of the genus. The very small seedling (Pl. 1, fig. 2) has the cotyledons raised above ground by a short but very distinct hypocotyl (H in fig. 2); the primary root (R) is long and very slender with a few ramifications, densely covered with root hairs. At this stage two leaves, succeeding the cotyledons, are already visible, and the plant is now ready to meet the first winter. The first sign of change in the equipment of this little plant is the loss of the cotyledons; thereupon follows a gradual wrinkling of the hypocotyl, by which the apical bud becomes pulled down beneath the surface of the ground, and the root continues its growth vertically and to a very considerable depth. In the following spring the leaves develop and form soon a small rosette, while the hypocotyl and the basal portion of the root has commenced to increase in thickness; lateral, slender roots become also developed. (Pl. 1, fig. 3.) How soon the flowering begins we do not know, but it is very likely that it takes the plant three or four years before it produces flowers.

In fully matured specimens the leafy rosette is very large, the hypocotyl still visible as a cylindric, thick, and prominently wrinkled body above a long, very fleshy, and thick root, the primary; the lateral roots persist also and increase quite considerably in thickness, but not to such an extent as the main root (Pl. 1, fig. 4). If we lay a longitudinal section through the rosette and the hypocotyl, we notice at once a number of small, young inflorescences and leaves ready to push out during next spring. These inflorescences are stalked and erect, and the young flowers are covered by the (fore) leaves. The hypocotyl persists during the whole life of the plant, and constitutes a portion of the wrinkled crown above the root. Characteristic of *C. megarrhiza* and *arctica* is, thus, the continuous growth in length and thickness of the primary root, besides the overwintering of the leaves and inflorescences.

It is now interesting to study the morphological structure of *C. Virginica* L., which no doubt is a near ally of *C. megarrhiza;* biologically, however, they are very distinct. Let us state at once that *C. Virginica* does agree with *C. megarrhiza* as far as concerns the monopodial shoot and the persisting primary root, though not the entire root. The development of the plant is as follows:

As already described by GRONOVIUS,[b] "Monocotyledonum instar protrudit unicum foliolum," and so is the only sign of the seedling above ground a single leaf with a small blade borne on a long, filiform petiole (Pl. 2, figs. 10 and 12). This leaf is borne upon a small tuberous body underground, which terminates into a long, filiform root (R in fig. 10) with a few ramifications and densely clothed with hairs. An anatomical study of the tuberous body shows at once that this is also a part of the root, and no hypocotyl is thus developed. The base of the petiole closely surrounds a minute leaf (*l'* in fig. 11), which sometimes develops during the first season (*l'* in fig. 13), and this leaf resembles the proper leaves of the full-grown plant. During the first season the base of the root increases rapidly in thickness, while the slender portion dies off and no trace of this is to be found in the following spring. The development of leaves continues at the same time as the root grows in thickness, forming a more or less globular body with many superficial, transverse wrinkles (Pl. 2, fig. 15), and with several long roots developing in small tufts from the sides. Some three or four years elapse before the flowers appear, and the fact that the floral stems are not preceded by a leafy rosette, as in the former species, makes it somewhat difficult to appreciate that the stems are actually axillary and that the shoot represents a monopodium. But if we examine the apex of the tuberous body—the root—we readily notice that the center is occupied by minute leaves and inflorescences, the position of which answers that of a monopodium and also that of a shoot of *C. megarrhiza*, with the exception that the leaves do not winter over in *C. Virginica.* In this way these two species show a marked distinction in respect to the persistence of the entire root and the overwintering of the leaves in *C. megarrhiza* in contrast to the reduction of the root and the early fading away of the leaves in *C. Virginica.*

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[a] The author: On the vitality of some annual plants. (Am. Journ. of Sci., vol. 42, 1891, p. 304.

[b] Flora Virginica, Pars. I, 1743, p. 25.

Judging from the appearance of the vegetative organs in *C. Caroliniana* and *C. lanceolata*, these two species show evidently the same course of development as we have observed in *C. Virginica;* but they ought to be studied.

The last perennial and monopodial species is *C. sarmentosa* Mey. (Pl. 1, figs. 5 and 6). This is nearest related to *C. megarrhiza* with which it has in common a long, perennial root, persisting in its entire length, and an overwintering rosette of leaves. But it differs, and very prominently so, by the main root being quite slender, by the leaf-bases being somewhat swollen, and by its ability to wander by means of stolons above ground, developed from the axils of the leaves, in our specimens of leaves from the previous year. The stolons consist either of one single internode terminated by a rosette of leaves (fig. 5), or they bear several long-petioled leaves with stretched internodes, preceding the terminal, vegetative bud (fig. 6). Secondary roots develop from the internodes of these stolons (*r* in figs. 5–6).

The successive development of inflorescences and leaves is, however, identical with that of *C. megarrhiza* and *C. Virginica.* We have thus in *C. sarmentosa* a truly stoloniferous species, yet with the primary root persisting as in the other species, and with the shoot being monopodial. Furthermore the monopodial structure of the primary axis becomes repeated in the axillary branches, the stolons.

These species, described above, represent then several types of rhizomes, but only a few of these are stoloniferous, and the plants show but a very limited ability to wander, for instance, *C. asarifolia* by its creeping rootstock, *C. sarmentosa* by its stolons, and *C. parvifolia* by its deciduous bulblets. We now pass to describe the vegetative propagation of *C. Chamissonis*, which in this particular respect appears to be the best equipped of all the members of the genus. Besides propagating by seeds, this species gives, also, an excellent illustration of a stoloniferous and bulbiferous plant. Our figure 7 on Pl. 1 shows a small specimen, the smallest we could find in order to represent the plant with its rhizome in natural size; nevertheless, it is perfectly sufficient for giving an idea of the mode of growth.

A flower-bearing shoot has developed from a bulb, and the stem above ground is terminated by a two-flowered inflorescence, preceded as usual by a pair of opposite leaves; but in contradistinction to most of the other *Claytoniæ*, the aerial stem is leafy from the base to the flowers, and all the leaves are opposite, including those of the subterranean stolons and bulbs. The root system is poorly developed, there being only some filiform, almost unbranched roots proceeding from the minute internodes of the bulb, from which the shoot has developed. Long and slender stolons with small, opposite, scale-like leaves are visible in the axils of the bulb scales and of one of the lowermost leaves of the stem; these stolons, which are often branched, are either terminated by a small, pointed bud or by an ovoid bulb with thick, fleshy scales of a crimson color. Both forms of stolons are underground, and they both send up an aerial shoot in the coming year. This kind of propagation takes place at a very early stage, already in the first year when the seed has germinated. Such seedlings show, thus, a pair of small, hairy cotyledons above ground, from the axils of which stolons develop. The immediate direction of these stolons was, however, vertical instead of horizontal, since they were developed in some distance above the surface of the ground, the cotyledons being epigeic, as described above; the primary root is quite long, but very thin and slightly ramified; its duration does not exceed one season, since the floral shoots always die off after the ripening of the seeds while the stolons and the bulbs winter over.

The structure of the seedling showed very plainly that the shoot is not monopodial but that it is terminated by an inflorescence, as in the specimens that had developed from stolons, as figured and described in the preceding.

If we now compare GRAY's systematic classification of the species with our table, based upon the structure of the shoot alone, it is evident that certain species, otherwise closely related, have become separated from each other and referred to distinct sections, in some instances to sections of their own—monotypic. The members of *Euclaytonia* have been divided, and both *C. sarmentosa* and *C. asarifolia* appear to be distinct from these and distinct among themselves. *Limnia*, on the other hand, stays unchanged, and so do the monotypic *Alsinastrum* and *Naiocrene*, besides *Montiastrum*. So, after all, the systematic classification compares fairly well with our arrangement of the species, and of the two the former is, no doubt, the most natural, even if some of the species may represent very distinct biological types.

Nevertheless, several analogies exist by which these types pass over into each other, and by which the genus becomes actually quite definite and naturally outlined. Not speaking of the uniformity in floral structure observed in all the species, the shoot itself, with its branches and root system, does also show some degree of uniformity, at least in a general way. The inflorescence is of the cymose type throughout the genus; the monopodial structure is common to nearly all the species, annuals as well as perennials; the primary root stays as a more or less typical taproot in most of the species; finally, the tendency of developing bulblets is well expressed in some of these plants.

## IV. THE ANATOMICAL STRUCTURE OF THE VEGETATIVE ORGANS.

While dried and pressed material may be sufficient to the study of a part of the morphological structure, it is seldom of much use for anatomical purpose, especially not when the plants are more or less succulent, as in the present genus. We therefore regret that our material preserved in alcohol only consists of a few species, collected from time to time; but whatever importance may be attached to the result of our investigation, a brief sketch of the anatomical peculiarities of some of these species may serve, at least, as a modest contribution to the knowledge of these plants heretofore but little known from this particular point of view.

### THE ROOT.

The somewhat modified structure of the roots in certain species necessitates the treatment of these to themselves. We may begin with *C. megarrhiza*. In this the ultimate ramifications of the lateral roots are the only ones wherein the primary arrangement of the tissues is still preserved and of which the structure is identical with that of a normal root. We notice here a hairy epidermis, covering a hypoderm of very wide cells, inside of which there is a cortical parenchyma, consisting of only two layers, the innermost differentiated as a thin-walled endodermis. The pericambium is similarly thin-walled and continuous, surrounding a central linear group of very narrow scalariform vessels and two groups of leptome, the elements of which are exceedingly narrow.

If we now examine the slender, apical portion of the primary root in its second or third year of growth, we notice a marked difference from the former by the absence of all the tissues from epidermis to the pericambium, inclusive. The root has grown in thickness, and the pericambium has now, by rapid cell division, developed several (about five) peripheral strata of cork and a secondary cortex, which consists of about twelve layers of starch-bearing cells. The innermost portion of the central cylinder shows a number of vessels, in the center of which the primordial are quite distinct from the younger by their narrow lumen. The leptome is located outside the wider vessels, separated from these by broad strata of cambial tissue, which extends also between the leptomatic groups themselves, thus covering the oldest part of the hadrome—the protohadrome vessels. This structure is, to some extent, also observable in the thickest roots.

But in these we notice a more or less distinct layering, like annual rings, which have been produced by the continuous formation of independent groups of leptome with a few vessels in the secondary cortex. These rays of collateral mestome-bundles are furthermore separated from each other by broad rays of pith. The central cylinder, with the primordial groups of leptome and hadrome, is hardly discernible in these thick roots; the entire central group of these tissues is mostly destroyed, and the root shows generally a broad, hollow center.

While examining some older roots of this species we often noticed that the long, lateral ramifications showed a tendency to grow together in several places, thence to become separated, and sometimes to grow together again at a greater depth (pl. 1, fig. 4). The complete preservation of the central cylinders in such roots, where they were free and where they had grown together, seems to prove that a fusion had actually taken place rather than a cleaving of a single root. Another peculiarity which was frequently observed in the very thickest portion of the root was that the internal structure did not only show one central cylinder with its heavy mass of secondary cortex, but also several much smaller and apparently independent mestome-cylinders. Considering the fact that each of these mestome-cylinders possessed exactly the same structure as that of a slender root, viz, that it was covered by several layers of cork surrounding a secondary cortex and a central portion of leptome, cambium, and vessels, make us believe that these represent lateral roots, and that they remain inclosed within the loose and very heavy coat of cork layers, which is always noticeable in matured roots of this species. In some cases, especially where several of these mestome-cylinders were massed together, some of these showed the same tendency to melt together as the free roots; but also in these were the central cylinders perfectly isolated, and the only tissues in which the fusion was observable was the cortex and the cork, the latter forming one single coat around two of these mestome-cylinders. The thick root of *C. megarrhiza* thus represents the primary root of the plant, and it persists for several years, with a gradual increase in thickness. The thickness, however, does not seem to be due only to the formation of secondary tissues within the main root alone, but also to the development of lateral roots, which not only increase in thickness themselves but which, furthermore, remain inclosed and covered by the cork of the primary root.

Similar cases of roots being inclosed has been described as characteristic of some other plants, for instance: *Bromeliaceæ*,[a] *Eriocaulaceæ*,[b] *and Ophrydeæ*.[c]

In *Claytonia Virginica* L., the underground, dark-brown, tuberous body from which the flowering stems and leaves proceed is generally described as a tuber, or sometimes as a corm, but, as stated above, this organ represents a root, the base of the primary. The long, filiform apex of the main root (Pl. 2, fig. 10) dies off during the first season, while the basal portion persists, and increases gradually in thickness; it soon becomes globular, but when it is fully matured it represents a more or less laterally compressed body, with a roundish outline. At this stage numerous filiform lateral roots are observable; they appear in small tufts on the edges of the mother root, which is yet very distinctly diarchic. The minor structure of these roots at their various stages is as follows: The lateral roots are of two kinds, some that are capillary, smooth, and almost unbranched, and others that are thicker, prominently wrinkled and ramified. Of these the latter develop from the central cylinder of the mother root, while the former appear as basal lateral ramifications of these. The wrinkled roots are able to increase in thickness, but only a little, and they never attain the swollen appearance of the mother root. Their increase in thickness depends upon the divisions of the pericambium developing a cork outward and a secondary cortex inward, throwing off the older tissues from the epidermis to the endodermis incl.; a cambial tissue has also developed to the same extent as described under *C. megarrhiza*.

The most noticeable characteristic of these roots is their contractile power, which is effected by means of a wrinkling of the cork layers, in which the radial cell walls show very distinct undulations. A much more simple structure is possessed by the smooth and slender ramifications. In these the original structure remains unchanged (Pl. 2, fig. 18). The hairy epidermis is thin-walled; the cortex (C in fig. 18), consists only of three layers, of which the innermost is differentiated as an endodermis (End. in fig. 18); the pericambium (P) is continuous, and surrounds two rays of hadrome alternating with two groups of leptome.

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[a] Jörgensen, A.: Bidrag til Rodens Naturhistorie (Bot. Tidsskr. Copenhagen, ser. 3, vol. 2. 1877–79. p. 150.

[b] The author: *Eriocaulon decangulare* L. (Bot. Gazette, vol. 31. 1901. p. 23).

[c] Same: The root structure of North American terrestrial *Orchideæ* (Am. Journ. of Sc., vol. 18. 1904. p. 208).

If we now examine the primary root we notice that the structure of its filiform apex, which only persists during the first season, agrees exactly with that of the capillary lateral roots, which have just been described. But the structure of the swollen base is different. In this the pericambium becomes gradually very active, besides that a cambium develops inside the leptome and extends from there around the primordial vessels. This increase continues from year to year, accompanied by the development of collateral mestome-bundles in the starch-bearing cortex. The mode of growth is like that observed in the main root of *C. megarrhiza*, though with the important distinction that in this species the apex continues to grow, while it dies off in *C. Virginica*. Moreover, in the latter species the central cylinder persists for a very considerable period, and the secondary cortex with its coat of cork layers remains active throughout the life of the plant. The lateral roots are quite numerous in both, but in *C. Virginica* they do not traverse the cortex vertically as fully developed roots, but they proceed at once to the periphery until they become free, as is the usual course followed by lateral roots.

A very long, but relatively slender, primary root is possessed by *C. sarmentosa*, and it persists for several years. It is not contractile, but combines the functions of a storage and a nutritive root. The increase in thickness is quite moderate, and the central cylinder, with its mass of narrow vessels and groups of leptome, does not break down even in the older roots, while the peripheral tissues become replaced by layers of cork and starch-bearing secondary cortex. Lateral roots occur, but they are scarce; the primordial tissues are all noticeable in these, even if some slight increase in thickness does take place; the endodermis is moderately thick-walled, and the pericambium is continuous.

If we now examine the root system of one of the annual species—for instance, *C. arenicola*—we notice that both the slender, main root and its almost capillary ramifications are able to grow in thickness.

The epidermis and hypoderm are thrown off very soon, together with the cortex, and are replaced by two or three layers of secondary cortex, surrounding the central cylinder of hadrome and leptome, besides some cambium. The lateral roots are all diarchic, but the very irregular position of the numerous (about thirty) narrow vessels in the primary root made the number of primordial rays indeterminable.

In species where an underground stem becomes developed—for instance in *C. parvifolia*, *C. asarifolia*, and *C. Chamissonis*—the primary root is no longer observable in matured specimens, but is replaced by secondary, which proceed from the short internodes. The structure of such roots is very simple, since they show no signs of increasing in thickness, and neither are they contractile. They have an epidermis with many hairs, directly covering a cortex of about five layers, inside of which is a thin-walled, or sometimes slightly thickened, endodermis; a continuous pericambium surrounds two distinct hadromatic rays, alternating with two groups of leptome.

In bringing these facts together it appears as if the root system of our species of *Claytonia*, represents four physiological types: Nutritive, attachment, contractile, and storage roots. Of these, the first type is well exemplified in the secondary roots of *C. parvifolia*, *C. asarifolia*, and *C. Chamissonis;* the second in the annual *C. arenicola;* the third in the slender lateral roots of *C. Virginica;* while a combination of both contractile and storage roots may be observed in the main root of *C. Virginica* and *C. megarrhiza*. In *C. sarmentosa*, on the other hand, the root seems to combine the function of a nutritive with that of a storage root.

### THE STEM.

The above-ground stem is of short duration in *Claytonia*, and lasts only one season. In some species it bears only two large green leaves and an inflorescence (*C. Virginica*, etc.), in others it bears several, but smaller, leaves, which are either alternate or opposite (*C. Chamissonis*), in the axils of which may be developed either inflorescences, vegetative shoots with distinct internodes, or small bulblets.

However, the stem structure is almost identical, and characteristic of the genus seems the lack of collenchymatic and stereomatic tissue, as mentioned by BECKER.[a] The cuticle is always distinct, and is prominently wrinkled in *C. Chamissonis*, *C. megarrhiza*, and *C. sarmentosa*. In regard to epidermis, we notice in *C. Virginica* (Pl. 2, fig. 17) an excessive thickening of the outer cell wall, with numerous layerings; in the other species the outer cell-wall is generally thickened, but only moderately. The cortical parenchyma is rather open from the intercellular spaces being quite wide, and the innermost stratum is differentiated as an endodermis, usually thin walled throughout, and showing the Casparyan spots very plainly; in *C. arenicola*, however, the endodermis showed the cell-walls slightly thickened. Inside the endodermis are four very broad collateral mestome-bundles, separated from each other by thin-walled parenchyma, medullary rays; besides that there is a narrow group of this same tissue in the center.

If we now compare the structure of the rhizomes, we find in the stolons of *C. Chamissonis* almost the same development of the various tissues as in the stem above ground. But in the stolons the cortex contains deposits of starch, and the endodermis has the inner cell-wall slightly thickened; besides that, there is some thick-walled mestome-parenchyma between the leptome and the endodermis. Of the four mestome bundles, the two are much broader than the others, and the pith seems to be less developed than in the stem. The stolons of this species possess no cambium, and are thus incapable of growing any further in thickness; they are not of any long duration, either, since they evidently separate from the mother plant at the close of the first season, when they are able to continue their growth independently.

A more developed structure is possessed by the above-ground stolons of *C. sarmentosa*. In these the cuticle is thick and prominently wrinkled, covering an epidermis of small but somewhat thick-walled cells; the cortex consists of about eight quite compact layers, but without starch. The thin-walled endodermis surrounds a secondary cortex of about six layers, with abundant deposits of starch, inside of which is a closed ring of several collateral mestome-bundles with intrafascicular layers of cambium. The center of the stolon is occupied by a narrow cylinder of starch-bearing pith. In this species the stolons are thus able to increase in thickness, and our material showed plainly that they remain active and in connection with the mother plant for at least two or three years.

The horizontally creeping rhizome of *C. asarifolia* persists for several years, and shows many layers of cork, forming a thick coating around a broad, starch-bearing parenchyma of a secondary cortex. The mestome-bundles are all collateral and arranged in a circle; they consist of leptome, cambium, and many narrow vessels, especially pitted ducts. A very compact, starch-bearing pith occupies the greater portion of the central cylinder.

In *C. parvifolia* there is also a horizontal rhizome, but this is partly above ground, and of a much weaker structure. The epidermis is at length thrown off without being replaced by any layers of cork, while the cortex and endodermis persist; the former of these contains chlorophyll. There are only five collateral mestome-bundles, without cambium, and these are separated from each other by rays of the broad central pith.

A somewhat greater diversity in regard to the structure is thus observable in the rhizome than in the flower-bearing stems, which is quite natural when we consider the various modifications exhibited by the former, viz: The perennial creeping rhizome of *C. asarifolia*, the annual stolons of *C. Chamissonis*, in contrast to the perennial ones of *C. sarmentosa*.

## THE LEAF.

We meet here with several, and quite important, modifications of structure, which is by no means surprising, when we remember that the leaves winter over in some species, *C. megarrhiza*, *C. arctica*, and *C. sarmentosa*, but die off in all the others before the summer has passed, not speaking of such leaves as are developed as mere bulb scales, in *C. Chamissonis*, for instance.

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[a] Becker C.: Beitrag zur vergleichenden Anatomie der Portulacaceen. Inaug. diss. München, 1895.

It may, therefore, be advisable to treat of some of these species by themselves, beginning with *C. Chamissonis*. The stem bears many pairs of opposite leaves, which are held in an almost vertical position, and their structure is as follows: The cuticle is distinct, wrinkled near the margins of the blade, but is otherwise smooth. The outer cell-walls of epidermis are moderately thickened, and the radial are more or less undulate, especially on the upper, the ventral face of the blade. Stomata abound on both faces; they are raised a little, and possess two subsidiary cells, which are parallel with the stoma, and the air chamber is wide and deep. No trichomes of any kind were observed, but small, stiff hairs were, nevertheless, observed upon the earliest leaves, succeeding the cotyledons. The chlorenchyma is differentiated into a typical palisade tissue on the ventral part of the blade, and as an open pneumatic tissue on the dorsal. No mechanical tissue, neither as stereome or collenchyma was observed, and the mestome-bundles are only surrounded by a thin-walled parenchyma sheath, and deeply imbedded in the chlorenchyma.

In the bulb-scales of this same species the thin-walled epidermis lacks, of course, stomata, and the mesophyll is merely represented as a homogenous tissue of closely packed roundish cells filled with starch. The mestome-bundles are very small and only three in number.

In *C. Virginica* the stomata are most abundant on the dorsal face of the blade, and they have often two pairs of parallel subsidiary cells instead of but one; moreover, the cells of the ventral epidermis are usually somewhat larger than those of the dorsal. In regard to the chlorenchyma, this shows the differentiation as in the former species, but the pneumatic tissue is still more open, on account of the very irregular shape of the cells, leaving very wide intercellular spaces. The mestome-bundles are also small in this species and are not supported by any kind of mechanical tissue. The basal leaves have very long and slender petioles, in which there is a chlorophyll-bearing cortex with very wide intercellular spaces, besides lacunes. There is one crescent-shaped central mestome-bundle and two small lateral, which are orbicular in transverse sections; each of these is surrounded by a special thin-walled endodermis.

If we now examine the overwintering leaf of *C. megarrhiza*, we notice in this a very thick and smooth cuticle, covering an epidermis, with the outer cell-walls prominently thickened, but perfectly glabrous. The stomata (Pl. 2, fig. 9) are somewhat raised, and possess mostly two pairs of subsidiary cells, more or less parallel with the stoma. They appear to be equally distributed on both faces of the blade. A thick homogenous parenchymatic tissue represents the chlorenchyma, the individual cells of which are shaped like palisades, vertical on the leaf blade and filled with chlorophyll. The mestome-bundles are small and deeply imbedded in this tissue. No support of mechanical tissue was observed.

Although the leaves of *C. sarmentosa* are green during the winter, thick and fleshy like those of *C. megarrhiza*, they nevertheless show a very different structure. The stomata are almost exclusively confined to the dorsal face, and the cuticle is very thin. In this species the chlorenchyma is plainly differentiated into a ventral palisade tissue and a dorsal pneumatic, which consists of irregularly branched cells, like those observed in *C. Virginica*. Otherwise the structure of the mestome-bundles, etc., is like that of the previously described species.

The isolateral leaf-structure exhibited by *C. megarrhiza* is a character that has been observed in several other alpine species, pertaining to remote genera; the prominent development of the chlorenchyma into a palisade tissue seems to confirm the general supposition that in alpine plants the assimilation governs the structure of the chlorenchyma. On the other hand, the plainly dorsiventral structure with the very open pneumatic tissue, as represented by *C. sarmentosa*, is a good illustration of a plant adapted to an atmosphere charged with excessive moisture. In this case the transpiration seems to be a more important factor than the assimilation, as far as concerns the differentiation of the chlorenchyma into both a palisade and a pneumatic tissue.

It is somewhat surprising to observe a very open pneumatic tissue in the leaf of *C. Virginica*, which is not an inhabitant of wet localities or is in any way exposed to a damp atmosphere. Nevertheless, the leaf-structure of this species is more open than that of *C. Chamissonis*, a plant that grows exclusively in very wet places—in beaver swamps or along creeks in the aspen zone of the Rocky Mountains, for instance. Such controversies in structural respect are frequent—very frequent, indeed—and the present knowledge of plant structures is yet much too incomplete to enable us to offer any plausible explanation.

It seems, however, as if the species of *Claytonia* which we have examined exhibit certain structures which may be regarded as generic; for instance, the absence of stereomatic and collenchymatic tissues, the structure of the stomata (in contrast to those of the monotypic *Montia*), the four mestome bundles in the stem, the diarchic root, the lack of trichomes, of reservoirs, etc. By considering the external morphological structure of the various organs, we meet also here with some certain degree of uniformity throughout, even if some of the species may be regarded as very distinct from a biological point of view.

Brookland, D. C., *October, 1904.*

## EXPLANATION OF PLATES.

### PLATE 1.

Fig. 1. Bulblet of *Claytonia parvifolia*, magnified.
Fig. 2. *Claytonia megarrhiza*, a seedling, natural size; Cot.=the cotyledons; H=the hypocotyl; R=the primary root.
Fig. 3. Same species in the second year, natural size; letters as above.
Fig. 4. Same species, but at a later stage, natural size; the lateral roots have grown together with the primary.
Fig. 5. *Claytonia sarmentosa*, natural size; *r*=a secondary root developed from the stolon.
Fig. 6. Same species; a leafy stolon, natural size; *r*=secondary roots.
Fig. 7. *Claytonia Chamissonis*, natural size, showing a plant developed from a bulb, and bearing three stolons, the one of which is terminated by a bulb.
Fig. 8. *Claytonia diffusa;* a stem-leaf, natural size.

### PLATE 2.

Fig. 9. Stomata of the leaf of *Claytonia megarrhiza*, ×360.
Fig. 10. *Claytonia Virginica*, a seedling, natural size; Cot.=the cotyledon; R=the primary root.
Fig. 11. Same species; the tuberous portion of the primary root; $l^1$=the first leaf succeeding the cotyledon (Cot.); *r*=lateral roots; magnified.
Fig. 12. Same species; the blade of the cotyledon, magnified.
Fig. 13. Same species; a seedling, showing the cotyledon and a proper leaf, $l^1$; natural size.
Fig. 14. Same species in its second year, where the filiform apex of the primary root has fallen off; letters as above; natural size.
Fig. 15. Same species, showing the globular, primary root (R) with several filiform, lateral roots of a specimen about four years old; magnified three times.
Fig. 16. Same species; the stomata of the leaf ×360.
Fig. 17. Same species; transverse section of the stem; Epid.=epidermis; Hyp.=the hypoderm. ×480.
Fig. 18. Same species; transverse section of a filiform, lateral root; Ep.=epidermis; C=cortex; End.=endodermis; P.=pericambium; L.=leptome. ×840.
Fig. 19. The diagram of the flower of *Montia rivularis;* A=the axis; $C^1$=the posterior, $C^2$=the anterior calyx-leaf; copied from Almquist (l.c.).

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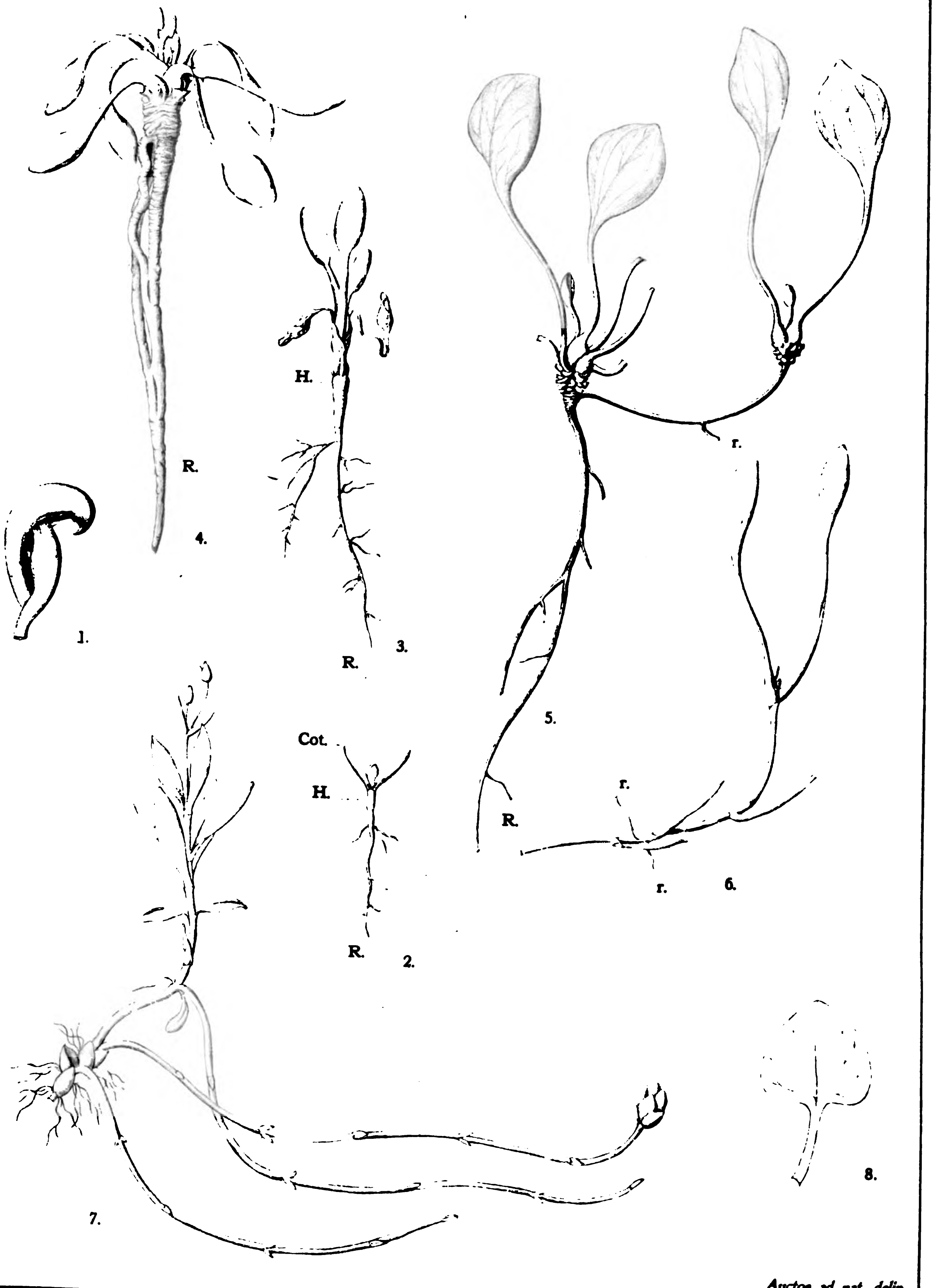
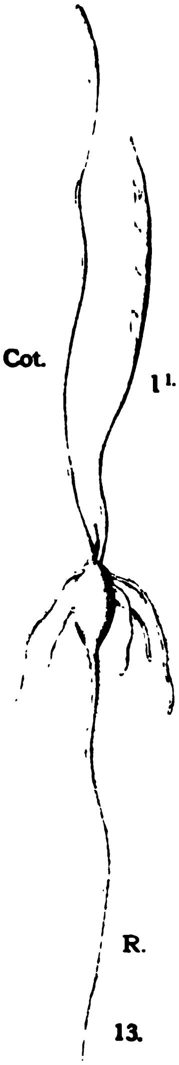


*Auctor ad nat. delin.*



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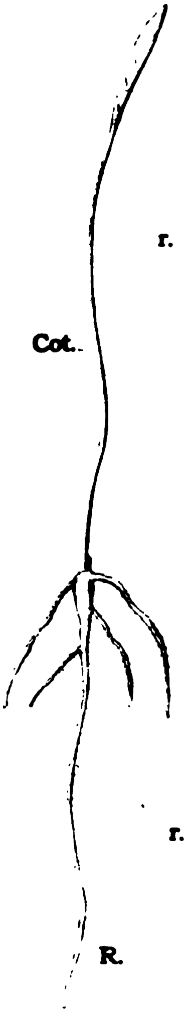

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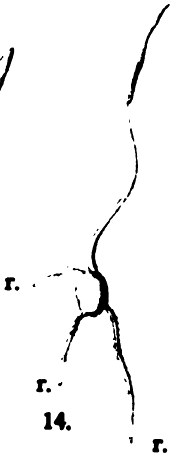

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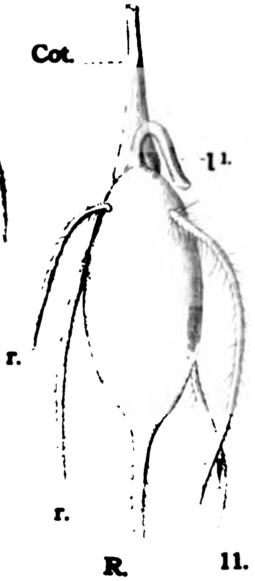

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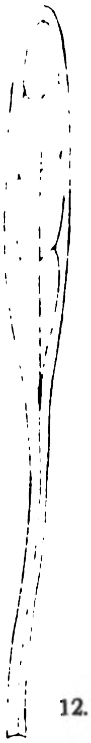

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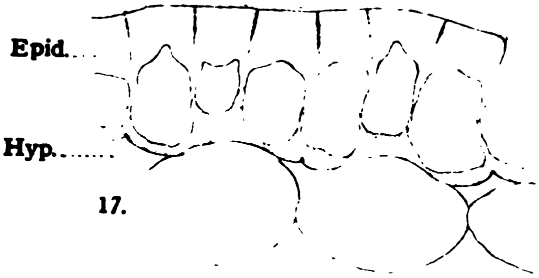

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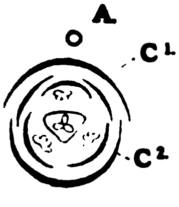

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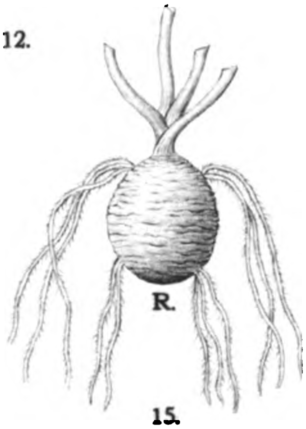

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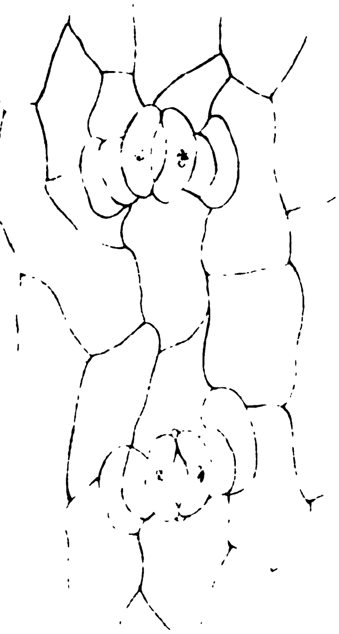

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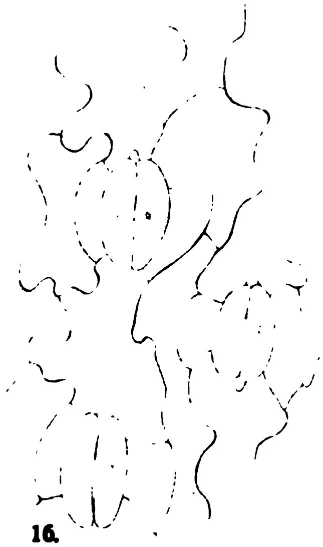

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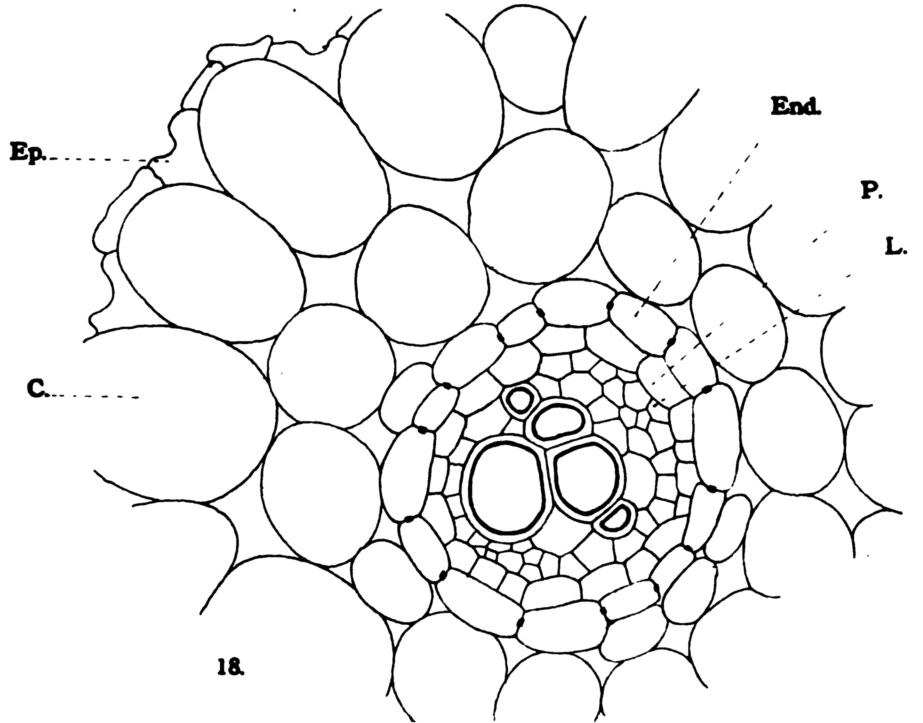

18.

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